ON DOMATIA IN CERTAIN AUSTRALIAN AND OTHER PLANTS.

By Alex. G. Hamilton.

(Plate lvii.)

Some years ago, when collecting *Pennantia Cunninghamii*, Miers, my attention was attracted by the presence of prominences on the upper surface of the leaves which I at first took to be the nidus of some leaf-mining insect larva. But further observation showed that they always had an opening on the under surface of the leaf, and invariably occurred in the same position, viz., in the axils of the veins. A short time after, I happened to look at the leaves of the ornamental New Zealand shrub, *Coprosma lucida*, commonly cultivated in gardens, and I was much interested to notice in this plant also the presence of cavities opening to the exterior by conspicuous pores on the lower surface of the leaf. After this I began to examine the leaves of the plants within reach more systematically.

No books that I was able to consult seemed to throw any light on the subject, and as I am distant from libraries, I was glad to make known my needs to several Sydney friends who were at length successful in giving me a clue.

The first important intelligence came from Mr. E. Betche, who sent me the following quotation from Dr. R. Schumann's article on Rubiaceæ, in Engler's "Naturliche Pflanzenfamilien":—"In den Nervenachseln auf der Rückseite der B. befinden sich zuweilen Haarbüschel, welche eine etwas eingedrückte Stelle der Blattspreite umwachsen; man nannte diese Stellen Blatt-scropheln (Scrobiculæ) gegenwärtig werden sie als Domatien bezeichnet. Sie sind fur gewisse Arten von *Cinchona* zur Unterscheidung benutzt worden."

The next difficulty encountered was to find definitions of scrobicula and domatium. Eventually Mr. J. J. Fletcher found in Henslow's "Floral Structures" (p. 115) a reference to Dr. Lund-

ström's important paper on the subject* (with a copy of which the author most kindly favoured me subsequently). Also that Howard (Illust. N. Quinologia) speaks of "the scrobicules or glands [in Cinchona], as Pavon calls them."

Mr. J. P. Hill sent me Geddes' "Chapters in Modern Botany," on p. 134 of which Lundström's views are mentioned. Mr. C. T. Musson obtained for me the reference to Mr. Cheeseman's paper "On the New Zealand Species of Coprosma,"† and so disposed of any doubt that New Zealand naturalists had failed to notice the structures in question in plants of this genus.

Dr. Lundström was the first naturalist who systematically investigated these structures. The following extracts from the summary of it in the Journ. R. Microscop. Soc. (1888, p. 87) will sufficiently indicate the conclusions at which he arrived in his valuable paper.

"Domatia.—Dr. A. N. Lundström defines as 'domatia' those formations or transformations on plants adapted to the habitation of guests, whether animal or vegetable, which are of service to the host, in contrast to cecidia, where such habitation is injurious to the plant. He describes these domatia in detail on the lime, alder, hazel, and other trees and shrubs, and gives a very long list of species, belonging to a great variety of natural orders, on which they are found.

"The principal types of shelter are as follows :—(1) Hair-tufts, *e.g.*, in *Tilia europœa*; (2) recurvatures or foldings in various parts, *e.g.*, in *Quercus robur* . . . ; (3) grooves without hairs, as in *Coffea arabica* . . . ; with marginal hairs, *e.g.*, *Psychotria daphnoides* . . . ; with basal hairs, as in *Anacardium occidentale* . . . ; (4) pockets, as in *Elæocarpus oblongus* . . . ; (5) pouches, *e.g. Eugenia australis*. These different types of domatia are connected by transition forms. The habit of producing domatia in a species may become hereditary without the actual presence of the predisposing cause. Certain orders,

* Nov. Act. R. Soc. Sc. Upsala, (3) xiii. (1887), pp. 1-72 (4 pls.).

† Trans. N. S. Inst. xix. 1886, p. 221 [1887].

e.g., *Rubiacea* (famous also for ant-domatia) show a marked predisposition to acaro-domatia. Many groups seem entirely without them, *e.g.*, Monocotyledons and Gymnosperms, and all herbs. They are most abundant and best developed in tropical (and temperate) zones.

"In the second chapter the author discusses in detail the various interpretations which may be put upon domatia. (1) They may be pathological, like galls; (2) they may be for catching insects; (3) they may have only an indirect connection with their tenants; (4) they may be of use to the plant as the dwellings of commensals. He adopts the last interpretation. He draws an interesting parallel, however, between galls and domatia, and is inclined to suppose that the domatia were first directly caused by the insects, but have gradually become inherent, transmitted characteristics. The author gives a clear table, distinguishing the cecidia or galls due to 'antagonistic symbiosis,' either plant or animal, (phyto- and zoo-cecidia), and domatia due to 'mutual symbiosis,' either plant or animal (phyto- and zoo-domatia). Those due to plants are again subdivided into myco- and phyco-cecidia or -domatia."

Mr. Cheeseman's remarks are very interesting, not only because his paper was published in the same year (1887) as Lundström's, but also because he, too, noticed that the domatia of *Coprosma* were often tenanted by Acarids. He says: "In nearly all the species except a few of the smaller-leaved ones, curious little pits exist on the under surface of the leaves, in the axils formed by the union of the primary veins with the midrib. They are never more than $\frac{1}{8}$ of an inch in length, and are usually much less. Inside they are lined with numerous stiff white hairs, which on being treated with caustic potash are seen to be composed of two or three cells. So far as I have observed, the pits do not secrete anything, and I am quite unable to guess at their function. They are often inhabited by a minute yellow Acarid, which makes use of them as a home. Sometimes two or three Acarids may be found in the same pit, and they crawl freely about the young leaves and branches." (Trans. N.Z. Inst. Vol. xix. p. 221.)

Lundström, quite reasonably, expresses surprise that domatia have attracted so little notice. And hardly less remarkable is it that up to the present time, the text books have still nothing, or so little to say about them or their significance. Nevertheless, they were long ago noticed in at least one Australian plant, but having been relegated to the category of "glands"—"that word of many meanings," as De Bary remarks—their nature seemed to be looked upon as settled. For example, in Vol. li. of Curtis's Botanical Magazine, published in 1824, there is a figure (Pl. 2488) of *Cissus* [*Vitis*] *antarctica* [= *V. Baudiniana*, F.v.M.], in which domatia are distinctly shown, while the text mentions "foliis ovatis laxe serratis glabriusculis subtus glandulosis." The synonymy also shows that at a still earlier period Poiret, because of the presence of these supposed glands, had described the species under the name of *C. glandulosa*, "foliis ovatis glabris laxe dentato-serratis nervis basi glandulosis."

In 1879, at a Meeting of the Linnean Society of London, "Mr. R. Irwin Lynch directed attention to a growing example from Kew Gardens, and some of the dried leaves of *Xanthosoma appendiculatum*, on the under surface of which peculiar pouch-like excrescences emanate from the midrib. This pseudo-monstrosity is of remarkably constant occurrence."* If these excrescences be, as I think they are, domatia, the plant (an Aroid) is remarkable as being the only instance known of the occurrence of domatia in the Monocotyledons. Mr. Lynch, too, is the first, apparently, who saw anything uncommon in the structures.

A few other references to what would now be called domatia may be given.

Trimen says of *Psychotria bisulcata*, "Lateral veins often with very deep pits in their axils, which appear as warts on the upper surface." ("Handbook of the Flora of Ceylon.")

---

* Journ. of Bot. April, 1879, p. 125, but not noticed in the Proceedings of the Society.

In classifying the Cinchonas, Howard states that Pavon divided the 40 species into two groups: 23 species without glands (sin glandulas) and 12 with glands (con glandulas). ("Illustrations of the Nueva Quinologia of Pavon," 1862.) *C. villosa*, one of the second group is thus described: "Folia . . . glandulis nonnullis rotundatis, subtus concavis, marginibus villosis, supra prominentibus, ad nervorum axillas insertis, supra obscure viridia, subtus dilute." . . . "This is a species moderately hairy all over, especially on the under-side veins." From the position of these so-called glands in the nerve-axils, and their appearance in the figures, I have no doubt but that they are domatia. Among the species spoken of as without glands, *C. viridifolia* is described as "At nerve-axils pilose-tomentose," which is one of the forms of domatia. *C. villosa* and *C. conglomerata* are mentioned as hairy. This is contrary to Dr. Lundström's experience: his opinion being that domatia do not occur in hairy-leaved plants.

A doubtful species of *Calisaya* known as "naranjada" is spoken of by Howard as having "scrobicules not only at the axils of the veins, but also at their junction with the smaller veins, as in *Olea scrobiculata*." The accompanying figure shows very distinct domatia, which are visible on both sides of the leaf. (Journal of Botany, 1869, p. 3.)

Of *Cinchona Ledgeriana*, Trimen says: "scrobicules not conspicuous, mostly confined to the upper vein-angles." (Journ. of Botany, 1881, p. 323.)

Martius in the "Flora of Brazil" refers to these structures in several descriptions of the leaves.

Hooker says of *Elæocarpus dentatus*, "with hollows where the veins meet the midrib." (Handbk. N.Z. Flora, p. 34).

F. v. Mueller remarks of *Cupania foveolata*: "The principal veins with dimples in their axils." (Fr. Phy. ix. p. 95.)

Bentham describes *Nephelium foveolatum* as "having frequently a cup-shaped cavity in the axils of the primary veins." (Fl. Aust. i. p. 466): *Cupania xylocarpa*, "with hairy tufts almost always conspicuous in the axils of the raised primary veins."

(*ib.* p. 447); the leaves of *Vitis oblongata* "with two large glands underneath in the axils of the lateral veins": the leaflets of *V. sterculifolia* "with glands or foveoleæ in the axils of some of the primary veins underneath" (*ib.* p. 450). He also mentions "glands" on the leaves of *V. Baudiniana*.

Recently G. de Lagerheim has described some new acarodomatia (2) in *Solanum jasminoides* and *S. pseudoquina*, and he refers to the descriptions in De Candolle's Prodromus as evidence of several other species being domatia-bearing: he also discusses a new form of domatium in some plants of the genus *Cestrum*.

A great part of the observations recorded below were embodied in a paper read at the Meeting of this Society in November, 1895, but as at this time I was not aware of Lundström's paper, I was allowed to withdraw it for the purpose of re-writing with a knowledge of that author's work.

The domatia that have come under my notice consist of hollows in the under surface of the leaf, and always occurring in vein axils. They are usually roofed over either by an extension of the leaf tissues, or by hairs. They are distinguished by peculiarities in the minute structure of the part of the leaf lying over them. Those that are known to me I divide into groups according to their outward structure as follows:—

Group i.—Circular lenticular cavities on the under side of the leaf, each with a small opening and a thickened rim. Those found in *Pennantia Cunninghamii* present the highest development of this type which I have seen.

Group ii.—Pouches formed by a widening of the principal and lateral veins at the axils, the space being filled in with tissue so as to form a triangular pouch or pocket. To this group belong the domatia in *Dysoxylum Fraserianum*.

Group iii.—Depressions or hollows formed by a thinning of the leaf substance at the axils. Of this type *Viburnum chinense* furnishes the best example.

Group iv.—Bunches of hairs in the axils proceeding from the principal and secondary veins, such as are found in *Rubus Moorei*.

Group v.—Thicker bunches of hairs at the axils in plants which have leaves coated with hairs, as in *Psychotria loniceroides.*

In groups i., ii. and iii. there may or may not be hairs in the domatium or round the edge of the orifice, or the hairs may be entirely absent. A regular gradation may be traced between all these forms, and it is sometimes difficult to say in which category a particular domatium should go. I think that this arrangement is the most natural, for as will be seen it is much the same as the consecutive steps in the development of the domatium of *Pennantia.**

Group. i.

Pennantia Cunninghamii, Miers.—In this plant, Domatia probably reach their highest development. They occur most commonly at the first axils of the secondary veins, but are sometimes to be found in the axils of the principals and secondaries, and very often on the ramifying veins at junctions (fig. 1). They vary from 9 to 50, and I have counted more than 100 on one or two leaves. They are very constant in occurrence. But some time ago I found two plants on opposite sides of a creek, and within a few yards of each other, in one of which every leaf had upwards of 30, while many on the other had none, and the majority only a few. But this was the only plant out of some hundreds which I examined that was in this condition. On recently visiting these plants, I find that all the young leaves on the plant formerly without domatia have them in normal numbers and perfect in development on the mature leaves. It will be seen

* Since completing this paper I have observed in *Mackaya bella*, Harv., (Acanthaceæ) rows of white hairs with crimson tips on the main and secondary veins at the axils; and triangular pouches in the leaves of *Eupatorium riparium*, Regel. (Compositæ). This last is interesting, as it is an herbaceous plant, in which Lundström supposed domatia did not occur. I have also received, through the kindness of Mr. R. T. Baker, herbarium specimens of *Weinmannia paniculosa*, F.v.M. (=*Ackama Muelleri*, Benth.), which possess the most remarkable domatia I have yet seen. I hope to describe these hereafter when I am able to examine fresh specimens. They certainly differ from the five types enumerated above.

that the absence of cavities in some species is a by no means uncommon occurrence, and Lundström and Lagerheim note the same fact.

The upper surface of the leaf is extremely glossy and dark green; the under side is duller and lighter in colour. When dipped in water, the upper wets readily, while the water gathers in patches on the under side, as if it were greasy. The pits appear on the upper surface as very distinct, though small, domed protuberances, circular or elliptical in outline (fig. 3); they are flatter on the under side (fig. 2). They vary in size in mature leaves from 1 to 3·5 mm. in diameter (outside measurement), and the depth is usually two-thirds of the diameter. The opening is small and usually circular, and in the largest about ·75 mm.; it is surrounded by a thickened rim in which are vascular bundles proceeding from the veins between which it occurs; the rim is lighter-coloured than the rest of the leaf. The interior is usually lined with 1-celled hairs. Stomates occur plentifully on the lower side of the leaf, but they are absent in the domatia and on the upper side of the leaf. The pits are often inhabited by minute Acari, and their ova and excrement are also found in them. The mites sometimes quit the cavities and wander about on the under surface of the leaf. I have also seen similar Acari in the stomatal cavities of *Banksia*, in the rolled leaves of *Ricinocarpus*, &c., and in any other cracks or cavities suitable for shelter in plants.

The microscopic examination of sections of the domatia cut at right angles to the midrib and vertically, as regards the blade of the leaf, shows the structure described below, which is pretty constant in all the domatia I have cut. Beginning at the upper surface of the leaf, *i.e.*, on the upper leaf-surface there are—

(1) The cuticle, which is thin (fig. 5*a*).

(2) An epidermis composed of one layer of small oblong cells (fig. 5*b*).

(3) A single layer of hypodermal cells (5*c*) much larger than those of the epidermis, and from elliptical to oblong in shape, with thickening at the angles. These cells are very thick-walled, and

in other parts of the leaf have little protoplasmic contents; but over the dome they are richer, and often contain chloroplasts. From their varying appearance in leaves of different ages I believe this layer is derived from the next below.

(4) The palisade-tissue (5*d*) consisting of two rows of short oblong cells, their long diameter being horizontal instead of vertical. These cells contain many (up to seven) very large chloroplasts.

(5) A layer of spongy parenchyma (5*f*) containing also very large chloroplasts. In this particular region this tissue can scarcely be termed spongy, as it is composed of oblong cells laid over each other like bricks in a wall; but away from the summit the cells are branching and form the usual network, and the most open part lies all round the perimeter of the cavity. The dense layer over the roof is characteristic of the domatia in all the plants I have examined. In the lamina, at a short distance from the cavity, the intercellular spaces are arranged perpendicularly, and extend from the lower epidermis to the palisade-tissue above, the stomata opening as usual into the spaces. All through the leaf in this region there are cells not to be distinguished in a fresh section, but which stain very deeply with any stain, and more especially with hæmatoxylin, they become quite opaque before the rest of the section is sufficiently stained (5*e*). These cells are very rich in tannin, and with ferric chloride give a greenish-black reaction. There are also ducts in the vascular bundles of the veins on each side of the cavity filled with the same substance. The tannin-sacs are arranged in two parallel layers, one just under the palisade-tissue, the other at the bottom of the layer of spongy parenchyma, and resting on the inferior epidermis. All round the domatia the two layers coalesce, and then open out again the upper set going into the roof and the lower to the floor, and extending right to the rim of the mouth. The lower layer is less continuous, and thinner than the upper.

(6) The inner epidermis of the cavity (5*g*) continuous with and similar to the epidermis of the rest of the under side, but thinner.

(7) The inner cuticle (5*h*). Through this penetrate unicellular hairs (fig. 10) which are epidermal outgrowths, and are thick-walled and destitute of contents. They are rarely septate as shown in the figure, but usually resemble those of *Coprosma lucida* (fig. 11). This cuticle, as above remarked, has no stomata.

The same layers, omitting the palisade-parenchyma, are met with in the floor of the cavity, but in reversed order, and in the rim is a vascular bundle composed of five or six vessels.

On examining leaves of various stages of growth, I find that in leaves 5-9 mm. in length, the domatia appear as slight hollows. In leaves 1-9 cm. long I find the hollow deeper, and a little tuft of hairs in the angle. These are of two kinds: the ordinary pointed hair (fig. 10) and short thick ones composed of four almost globular cells. In a leaf of 4 cm. long a thickening is apparent along the sides of the veins, making a triangular pocket as in Group ii., and the hairs project from this. At 5 cm. long the thickening begins to extend across the mouth from the sides, so that there is a hollow surrounded by a ridge. Up to this stage the whole of the under side of the leaf is a purplish-brown in colour, but the ridge is a very bright green. The ridge had grown higher all round in leaves 5-5 cm. long, and a few hairs had grown on the front part of the ridge, their points directed towards the centre of the hollow. In leaves 6 cm. long the greater height makes the cavity appear much deeper. At 8 cm. the ridge has reached its full height, and there are a few hairs on the outside of the ridge—simple and pointed. The domatia are completely formed when the leaf is 11 cm. long, and no further alteration takes place except that in leaves a year old there are fewer hairs in the interior of the domatium. The leaves reach a length, when full grown, of 16 cm. and upwards. In examining a large series of young leaves, I found no Acari present until the domatium was fully formed. This fact has an important bearing on Dr. Lundström's theory of the meaning of the structures.

Coprosma lucida, Forst.—This plant also belongs to Group i. The domatia are very large and highly developed. They occur in the axils of the secondary veins and midrib, in pairs, or

alternately. They vary in number from 3-8. They rarely occur in the forks of the secondary veins. The leaf is very dark green, and has a varnished upper surface; it is lighter in colour and duller below. It wets readily on the upper side, but is greasy on the under side. It is very thick, fleshy and soft, and the rim of the cavities does not project beyond the veins as in *Pennantia*. They show above as slight rounded projections and have a round orifice below, surrounded by a slightly thickened rim, the thickening being internal. Internally they are lenticular, 2-3 mm. in external diameter and the opening ·5-1 mm. The interior cavity is proportionately smaller than in *Pennantia*. The rim is lighter in colour than the rest of the under surface. The interior is lined with thick-walled unicellular hairs (fig. 11), and hairs of the same kind occur on the midrib below, sparsely on its upper surface, and very plentifully in the channel of the petiole in young leaves. A section of the cavity perpendicular to the plane of the leaf and across the axis of the cavity shows the following structure, beginning on the roof—the upper surface of the leaf:—

(1) The cuticle.

(2) The epidermis, composed of one layer of small elliptical or oblong thick-walled cells.

(3) A single hypodermal layer of oblong cells with thickened walls, and almost always without protoplasmic contents.

(4) The palisade-parenchyma, made up of four or five rows of oblong cells little longer than wide, and very rich in chromatophores, sometimes as many as 20 lining a single cell. Besides these, there is often a highly refractive globule, yellowish-green in colour, and like an oil drop, which dissolves in ether and is probably a resin or oil. The cells of the highest row are much larger than those of the lower ones, each succeeding layer being of smaller cells. The outer cells are here and there empty, and occasionally a whole row is in this state, and then, except for the vertical position, they resemble the hypodermal layer, and as in *Pennantia* the latter appears to be derived from them. Under this lies:—

(5) A thick layer of spongy parenchyma, arranged in a network, but very closely, and with few intercellular spaces, and these very small. The cells of this layer are small. At the sides of the cavity they are larger and looser in arrangement, so that the perimeter of the cavity is surrounded by this more open network of cells, which gradually passes into the ordinary spongy parenchyma of the rest of the leaf. Here the intercellular spaces are regularly arranged, and extend from the lower epidermis to the palisade-tissue. These cells also have very many chloroplasts, and those nearest to the palisade cells have the oil globules above mentioned. But there are none of the tannin-sacs noted in *Pennantia*, and in the densest part they are never arranged like brickwork as in that species.

(6) A single layer of epidermis, the cells thick-walled, and the cavity circular in outline. From this proceed the unicellular thick-walled hairs springing from much enlarged cells, and sometimes but rarely septate.

(7) The cuticle of the inside continuous with that of the lower side of the leaf. No stomata occur in the cavity, but they are found up to the very margin of the orifice. Vascular bundles occur in the spongy parenchyma all round the cavity.

In the floor of the cavity all these layers except the palisade-tissue and the hypoderma occur in reversed order. The development of the domatia in young leaves takes place much as in *Pennantia*, but the unicellular hairs appear later, only the 4-celled hairs being present at first.

The points of resemblance between *Pennantia* and *Coprosma* are the dense spongy parenchyma over the roof and round the cavity, and the epidermal hairs inside and at the mouth. The differences are the occurrence of tannin-sacs in *Pennantia* and not in *Coprosma*, and the non-occurrence of oil globules in the cells, and of hairs on the outside of the leaves in the former.

Coprosma fœtidissima, Forst.—I have seen dried leaves only of this and the following seven species, and am not able therefore to give particulars of the minute structure. In this species the domatia are in the axils of the second and third pairs of veins

with the principal vein, and are from 2-4 in number. They resemble those of *C. lucida* externally.

C. HIRTELLA, Labill.—These resemble the last, but are small.

C. CUNNINGHAMII, Hook. f.—The domatia are small but otherwise like those of *C. lucida*.

C. SPATHULATA, A. Cunn.—As might be expected from the small size of the leaf, the 2-4 domatia are very minute.

C. BAUERIANA, Hook. f.—Dr. Lundström, speaking from observation of cultivated plants, says that the domatia in this species are hairless. I find that my notes afford no indication of whether hairs are present in the herbarium specimens I examined. I have simply noted that they resemble those of *C. lucida*.

C. GRANDIFLORA, Hook. f.—The domatia are long and the openings slits parallel to the midrib.

CANTHIUM LUCIDUM, Hook. et Arn.—The pits are situated in the axils of the second pair of veins and the midrib, and rather high up in the forks. They are two in all I have seen, but Mr. E. Betche informs me that they are often entirely absent. The leaf is a very glossy one. The openings are circular, about 1 mm. in diameter, the rim is raised and light-coloured, and vessels occur in it. So far as I can see there are no hairs present.

C. OLEIFOLIUM, Hook.—The leaf is evidently fleshy, and in the 'Handbook of the Flora of N.S.W.' is said to be "scarcely shining." The pouches are situated in the axils of the first and second pairs of veins and midrib, and are slightly alternate; they are 4 in number, but as in the preceding species are not constant. The opening is triangular or circular, and the rim is thickened and contains vessels. No hairs were seen in the interior.

RANDIA MOOREI, F.v.M.—The domatia in the leaf of this plant are minute. They are in the usual position, and are four or five in number. There is a prominence on the upper side of the leaf, and the thickened rim round the orifice on the lower side forms a conical mound, on the summit of which is the small opening. There are no hairs either round the mouth or in the interior. The microscopic structure is rather remarkable. There are :—

(1) The cuticle, which does not differ from that elsewhere on the leaf.

(2) A thick-walled epidermis, the cells often containing protoplasm.

(3) A row of bottle-shaped cells, of very large size, arranged touching each other at their large ends, but with spaces between the necks, which point to the mesophyll (fig. 14*a*). This occurs over all the leaf.

(4) The palisade-tissue which fills in between the necks of the bottle-like cells and below them. This is moderately dense, and the cells full of chloroplasts.

(5) A layer of close spongy parenchyma, which in all parts of the leaf is penetrated a little above the lower epidermis by

(6) A layer of thick-walled apparently empty cells (fig. 14*b*), which stain very deeply, and are, I think, 4-armed, as whether sections are made parallel, or at right angles to the midrib, cut ends are seen, circular and thick-walled. Both these and the bottle cells give a bright purple with ferric chloride, and are most likely tannin-sacs as in *Pennantia*. In fresh sections both kinds of cells are transparent and colourless, but in old spirit specimens they are bright brown. This layer divides in the same way as that in *Pennantia*, one part going to the roof and the other to the floor of the domatium. Those above are of normal size, while those below are smaller and more scattered.

(7) The epidermis resembling that of the upper surface.

The roof and floor of the domatia are irregular, almost papillose, and stomata occur in great numbers on the elevations. Vessels are present in all the walls.

R. STIPULARIS, F.v.M.—The leaf is very large, thick, fleshy and shining, and has very thick veins. The cavities are small and closely covered inside with hairs like those of *Coprosma*. These all point towards the orifice, so that looking down into it a close mat of points fills up the opening. This last is small and elliptical.

The epidermis is thick-walled; the palisade-parenchyma is composed of 5 or 6 rows of small oval cells closely packed; the spongy

parenchyma is also composed of oval cells, with small and few intercellular spaces. The hairs have an enlarged cell at the base and are thick-walled and destitute of contents.

R. CHARTACEA, F.v.M.—In herbarium specimens imperfect domatia, and bunches of hairs were seen in the axils of midrib and secondary veins, but fresh leaves showed no sign of them. I cut sections through the axils and found a few minute hairs, but no approach to the characteristic structure described in the foregoing species. I was struck, however, by the packing of large collenchyma cells on the upper side of the midrib and veins. These stained very deeply, and when tested with ferric chloride gave the same purple reaction as *R. Moorei*.

MORINDA JASMINOIDES, Cunn.—This is a climbing plant. The cavities are usually high up in the axils of the third pair of veins and midrib. They are opposite or alternate. There are from one to four, but are sometimes absent. The leaves are rather thin, dark green, but not very glossy. The domatia project very much on the upper side of the leaf, and but slightly on the lower. They are very large, and look like blisters or galls externally. They vary from 1-5 mm. long. The openings are sometimes of the full size of the cavity, but usually they are small and circular. There is sometimes a ridge parallel with the vein, thus forming a channel leading to the orifice. The rim is slightly thickened and lighter-coloured than the rest of the leaf. Many vessels occur in it and in the roof. Ordinarily there are no hairs on the interior, which is quite smooth and has large stomata in all parts. The minute structure, as seen in transverse sections, differs somewhat from that found in the previous plant. Beginning as before at the summit of the roof on the upper surface of the leaf, we meet with :—

(1) A thin cuticle.

(2) An epidermis here composed of very large oblong cells with thin walls, the longer diameter being horizontal. But over the rest of the lamina, the cells are longer vertically, and of great depth in proportion to the mesophyll. The upper and lower

epidermis taken together are as thick as, or thicker than the layers between. The epidermal cells are very clear and free from contents.

(3) The palisade-parenchyma composed of two rows of very small oblong cells. the inner row smaller and rounder than the outer and very closely packed.

(4) A very dense spongy parenchyma, becoming more open near the domatium. Both this and the palisade layer are very dense all through the leaf and very full of chlorophyll bodies, so that it is difficult even in the thinnest sections to make out the structure. I found hydrate of chloral most useful in clearing the sections.

(5) The epidermis of the domatium, in two layers, the inner composed of larger cells.

(6) The inner cuticle, through which stomata open in all parts of the cavity. The same layers occur in reverse order in the floor, and running from the midrib and vein is an extension of the round strengthening cells which occur outside these.

The above is a description of the domatium in an ordinary healthy state. I have rarely seen Acari in them. But some time ago I came across a plant with very large domatia which were evidently in an unhealthy state, being pale or brown, or even black. On examining them, I found that all the unhealthy domatia contained numbers of Acari and their ova. Sections of these showed the palisade and spongy parenchyma cells greatly swollen and very irregular in shape, and undistinguishable from each other. Brownish patches occurred here and there, and also in places a number of cells had taken a bright crimson colour. In some of the cells of the mesophyll there was a deposit of granular matter on the walls. The epidermal cells were normal as to shape, but even larger than ordinary. Where ova rested on the interior of the domatium, the cells were dark-coloured and very closely placed. At the mouth, hairs of the same kind as in *Pennantia* were placed. In three sections from the same domatium I counted ninety-two ova, besides several young and mature Acari.

The mites were the same species as are usually found in domatia. They appear to be very near, if not identical with, the *Gamasus* figured by Lundström. There could not be any doubt but that the mites had an injurious effect, and this, with another case to be referred to, was the only instance I have seen of the little animals being hurtful to the plant. But there was no sign of the peculiar alterations and structures which are caused by *Phytoptus* and some other noxious mites.

Tarrietia actinophylla, C. Moore.—The leaves are digitately compound, and when young are studded with star-shaped peltate hairs, especially on the midrib. The domatia are in the leaflets in the axils of the secondary veins and the midribs. They do not occur in the lower part of the leaflet nor near its tip. In the same leaflet some veins are in pairs opposite, and others alternate; the domatia thus are in pairs or single. In three leaflets examined by me there were 14, 15 and 17. The leaf is strong in texture and smooth, shining on the upper surface, but not varnished. It wets readily on this side, but on the lower surface the water runs together and passes down the vein channels; it does not, however, enter the domatia, as the orifice is too small. The pits are formed by a widening of vein and midrib running out towards each other and almost meeting in the centre (fig. 15), thus forming a depression leading into the domatium. Sometimes, however, the ridges meet, and then the mouth is circular. I have, therefore, put this form in Group i. although it really is transitional between i. and ii. The thickened part is lighter in colour than the rest of the under side of the leaf. There are no stomata on the upper surface, but they are plentiful below and of small size. None are found in the interior of the domatium. The latter are 1-2 mm. in diameter. Vascular bundles are plentiful in both walls and rim. The interior is lined with stiff hairs like those of *Coprosma*, the points all being directed to the orifice. Acari were observed in the domatia. The layers in a section of the pit were as follows:—

(1) A rather thick cuticle.

(2) The epidermis, the cells thick-walled and with bright brown contents which give the tannin reaction faintly with ferric chloride.

(3) The palisade-parenchyma, consisting of long cells, arranged in two layers, and very full of chloroplasts.

(4) The spongy parenchyma, denser here than elsewhere in the leaf, but yet more open than in *Pennantia* or *Coprosma*. It has a layer of tannin-sacs, but not very rich in tannin.

(5) The inner epidermis, thick-walled and with brown contents.

(6) The cuticle, through which project hairs, without stomata. The floor has cuticle, epidermis, spongy parenchyma (denser than that in the roof), epidermis, and outer cuticle. The stomata in the lower epidermis extend to the very edge of the mouth.

The brown contents of the epidermal cells are found all over the leaf, and appear solid and squarish in outline. The hairs of the domatium have also brown contents, often broken up so as to resemble a string of beads.

Vitex littoralis, Forst.—Mr. E. Betche discovered that the herbarium specimens of this plant in the museum of the Sydney Botanical Gardens, collected in New Zealand by Mr. T. Kirk, have well marked domatia, but on examining the growing plant in the gardens none could be seen. Many domatia-bearing plants show this inconstancy, but I have not been able to trace the cause. It must be remembered, however, that young leaves show nothing but the depression in the angle, to the naked eye, or even to the hand lens. In this way I think it happened that a plant of *Hodgkinsonia* to be referred to was recorded as being without these structures. From the above causes I am compelled to speak only of dried material of this species. The opening is circular, the rim very much thickened, and the domatium projects beyond the surface of the leaf both above and below. They are placed in the main axils and are 4-8 in number. I attempted sections after prolonged soaking in glycerine with a little spirit, and succeeded in cutting them fairly thin, but the cells were much distorted, and I could only see that the arrangement of layers resembled that in other plants, and that there were no hairs in the cavity or round the orifice.

Psychotria Carronis, C. Moore, et F.v.M.—I have seen only herbarium specimens of this plant. The domatia occur in the

main axils and are very large, with a wide elliptical opening. I could see no hairs present anywhere.

P. CYMOSA, Ruiz. et Pav.—The pouches occur in the principal axils and have a circular opening. The microscopic structure resembles that of *Coprosma lucida*, having the same dense layers of palisade-tissue composed of small cells very rich in chromatophores. The hairs are different, being septate, with as many as thirteen divisions (fig. 9). They have little or no cell contents. There are no stomata in the cavities.

P. BISULCATA, .—I have not seen this plant, and I am indebted to Mr. E. Betche for the information that Trimen (3) says of the leaf, "Lateral veins often with deep pits in their axils, which appear as warts on the upper surface."

The above-mentioned plants are all in which I have seen this highly developed form of domatium, but Lundström (1) describes a large number of other species which have it, mostly Australian.

Group ii.

DYSOXYLUM FRASERIANUM, Benth.—The domatia are in the principal axils of the leaf or leaflet; and, so far as I have seen, this form never occurs in the secondaries. Sometimes they are found on only one side of the midrib, but generally on both. They vary in number from one to twelve. The leaves of a plant growing in a shady situation are very dark green and shining, on the under side lighter. From a sunny spot, they are much lighter in colour and smaller. The leaf wets readily on the upper side, but is greasy below. The pits do not appear much on the upper side of the leaf, but on the lower side they are very prominent, sometimes projecting above the leaf surface 3 mm., and then are corky and diseased-looking. The size is on an average 3×2 mm. The opening is wide and arched (fig. 6). Vessels occur in the walls. The interior is hairy, the points of the hairs projecting from the mouth. There are no stomata inside the domatium.

The substance of the domatium roof consists of—(1) cuticle; (2) epidermis; (3) close palisade-tissue in two layers of very narrow cells, which are nearer the normal shape and arrangement

than any I have seen in other plants; (4) close spongy parenchyma; (5) epidermis; and (6) cuticle. Here and there in the spongy parenchyma occur spherical interspaces of large size and destitute of contents. In the diseased-looking domatia of great thickness I found that the spongy parenchyma layer was of greater thickness, the hairs absent, and the roof and floor epidermal cells filled with a red substance which formed a thick layer on both roof and floor. I fancy that this diseased state is caused by some insect (not a mite); taking up its abode in the domatia as I repeatedly found remains in sections of some rather large insect. The mites were found in a few of the domatia, and in all the domatia were found dust, pollen grains, and both spores and mycelium of fungi. It is rather remarkable that these should be so plentiful, as from the mouth opening towards the apex of the leaf, and the leaf itself having a horizontal position, they could scarcely be washed in by rain, especially as they are on the under side of the leaf. I did not find such quantities of foreign matter in any other domatia, even of those with orifices as large. But Dr. Lundström notes the same kind of thing in many species examined by him.

Cedrela australis, F.v.M.—The domatia are like those of the last plant, but flatter; stomata occur in the inside and there are none of the spherical intercellular spaces mentioned above.

In very young leaves (10 × 1·5 mm.) the under side of the leaf is covered all over with hairs; as the leaf grows older, the hairs drop off, except those in the axils where domatia are to form. The hairs are of two kinds, pointed and thin, and short 4-celled hairs filled with bright brown matter. These persist for some time on the general leaf surface, and in the axils. They are probably colleters. In a leaf 10 × 3 mm. I found the hair tufts and a slight widening of the veins in the axils, and in larger-sized leaves the tissue widens progressively. But the domatia have not reached their full development even when the leaf is full grown as to size. It is only when the leaf has gained its mature hardness and consistency that the process of growth in the domatia is complete.

ELÆOCARPUS GRANDIS, F.v.M.
E. CYANEUS, Ait.
ELÆOCARPUS LONGIFOLIUS, C. Moore

The domatia of these three species resemble those already described under *Dysoxylum* and *Cedrela*, but *E. grandis* has very long slender hairs, and *E. cyaneus* has none.

HODGKINSONIA OVATIFLORA, F.v.M.—Herbarium specimens of this plant showed very distinct bunches of hairs in the axils, especially one taken from a cultivated plant in the Sydney Botanical Gardens. But on examining fresh leaves (young) from the same plant, no hairs could be seen with a hand lens. I cut some sections of the axils, however, and found that a very small hairy depression did exist, and examination of numbers of sections revealed a slight extension of tissue from vein to midrib. I have no doubt, therefore, that mature leaves of the plant would show that it should be placed in Group ii. The hairs are few in number, straight and septate.

VITIS BAUDINIANA, F.v.M.—I have placed this form in Group ii. because though ordinarily it presents a marked difference in the shape of the triangular pouch, yet it is a modification of that shape, and in addition, all stages may be found from the triangular form almost to the sunken cavity with a circular orifice. They occur in the axils of the lateral veins and midrib, but are frequently present in the secondary vein-axils also, two or three on one vein. At the base of the leaf there are on each side of the midrib, first a small, and next a large lateral springing from the insertion of the petiole, and here are found four large domatia. In the whole leaf they vary from 8 to 30, or probably many more. I have never found them entirely absent in any leaf. The leaf is hairy, more especially on the under side and in the younger stages. It is easily wetted on both sides, but the water runs into greasy patches on the upper surface. The domatia are formed by the extension of tissue from the midrib and vein, but in the middle the extension grows out into a point, which arches over the mouth (fig. 7). In the centre, too, there is a dome formed by the

arching of the tissues. There is also sometimes a closed-in cavity on each side of the domatium. This I have seen in *Morinda jasminoides* also. The domatium is 2 mm. high, and the transverse measurement 2·5 mm. in large specimens. The interior is thickly lined with thin cottony hairs, and there are besides stalked T-shaped hairs (fig. 8). Stomata are found only in the lower epidermis, and do not extend to the cavity. I have often found in the domatia small hemipterous insects, which apparently are in the habit of frequenting the cavities, for when driven out of one they go straight to another.

The microscopic structure is much like that in *Dysoxylum*. The palisade-cells occupy half the thickness of the leaf. There is no thickening or thinning of the leaf blade at the domatium, but it curves upward slightly, showing a slight protuberance on the upper surface. Vessels occur in the domatium walls. It is difficult to make out the domatia in young leaves on account of the thick felty layer of hairs. But even in the bud stage I could make out that the tissue extension is present. I have not seen this so early in any other plant.

Group iii.

Viburnum Chinense, Hook.—The depressions are large and occur in the axils of midrib and veins. They are 6-14 in number. The leaf is thick in texture, light green, but not glossy. The depression is formed by a thinning of the leaf substance, and has sloping sides and an irregular surface. There is a slight thickening of the leaf all round the hollow (fig. 13), and on this and the elevations are tufts of light brown and curled hairs. They are thick-walled, and their contents are arranged in globules like a string of beads. On the thinner veins where there are no domatia a few rows of straight hairs grow. The hollows are about 2 mm. in diameter. Stomates occur on the lower surface of the leaf and in the hollows. The minute structure is as follows:—(1) Cuticle; (2) epidermis of the upper surface with thick walls; the cells containing a considerable amount of light green chlorophyll; (3) palisade-tissue very full of large chromatophores, passing gradually

into (4) a very loose spongy parenchyma also rich in chlorophyll, the cells large in size, and staining deeply; (5) a thick-walled epidermis sometimes having brown contents as in *Tarrietia*, out of which grow the hairs, two, three or more hairs springing from one cell (fig. 13); (6) the cuticle with stomata.

Sloanea Woollsii, F.v.M.—The depressions are in the axils of the midrib and laterals, and begin at the lowest pair. They number 15-21, and are minute—1 mm. in diameter. The leaf is hard in texture and smooth; it wets readily above, but on the under side the water runs into patches. There is not such a decided thinning of the leaf as in *Viburnum*, but the thickened rim runs all round, and few hairs grew on this. Stomata are found on the under surface, but, so far as I can see, none extend to the hollow. The microscopic structure is as in the last-named species, except that there are no deeply staining cells, and the spongy parenchyma becomes very dense over the roof.

Gardenia sp.—In a commonly cultivated species of this plant I found depressions filled in with long straight hairs springing from the vein and midrib: they are roughened on the surface, septate, and have green or brown contents at the tip. Stomata occur in the pit.

Group iv.

Examples are seen in *Hydrangea hortensis*, Sieb., *Morinda citrifolia*, Linn., and *Mandevillea* sp.hort. There is nothing resembling the microscopic structure of the cavities, etc., to be seen in these. The cells from which the hairs spring in *Mandevillea* are bright crimson. I have also seen them in *Prunus Lusitanica*, Linn., *P. domestica*, Linn., *Rubus Moorei*, F.v.M., *Solanum* sp.hort., and some other plants, but I have not made sections of these.

Group v.

The only plants which I have seen, hairy all over but having a thicker tuft in the axils, are *Psychotria loniceroides*, Sieb., and *Diploglottis Cunninghamii*, Hook. f.

I have described the domatia of the above-named species fully as types of the structures in question. The following list of domatia-bearing plants which I have myself examined is arranged according to Natural Orders. I have followed Baron von Mueller's arrangement in the Second Systematic Census of Australian Plants.

MELIACEÆ.

Dysoxylum Fraserianum, Benth.	ii.
Synoum glandulosum, A. de Juss.	ii.
Cedrela australis, F.v.M.	ii.

STERCULIACEÆ.

Tarrietia actinophylla, C. Moore	i

TILIACEÆ.

Elæocarpus cyaneus, Ait.	ii.
grandis, F.v.M.	ii.
obovatus, G. Don.	ii.*
Sloanea Woollsii, F.v.M.	iii.

SAPINDACEÆ.

Diploglottis Cunninghamii, Hook. f.	v.
Nephelium foveolatum, F.v.M.	ii.
Beckleri, Benth.	ii.
Harpullia Wadsworthii, F.v.M.	ii.†

ROSACEÆ.

Rubus Moorei, F.v.M.	iv.
Prunus Lusitanica, Linn.	iv.
domestica, Linn.	iv.

---

* Probably the species *E. foveolatus* was named from the presence of domatia. I have not seen it.

† *Cupania foveolata*, F.v.M., is described as having dimples in the axils.

SAXIFRAGEÆ.

Hydrangea hortensis, Sieb. ..... iv.

VINIFERÆ.

Vitis Baudiniana, F.v.M. ..... ii.

ARALIACEÆ.

Panax elegans, C. Moore et F.v.M. ..... ii.

OLACINEÆ.

Pennantia Cunninghamii, Miers ..... i.

RUBIACEÆ.

Gardenia sp.hort. ..... iii.
Randia chartacea, F.v.M. ..... i.
Moorei, F.v.M. ..... i.
stipularis, F.v.M. ..... i.
densiflora, Benth. ..... iv.
Hodgkinsonia ovatiflora, F.v.M. ..... iv.
Canthium oleifolium, Hook. ..... i.
lucidum, Hook. et Arn. ..... i.
Morinda citrifolia, Linn ..... iv.
jasminoides, Cunn. ..... i.
Psychotria cymosa, Ruiz. et Pav. ..... i.
loniceroides, Sieb. ..... v.
Carronis, C. Moore et F.v.M. ..... i.
Coprosma lucida, Forst. ..... i.
robusta, Raoul ..... i.
grandiflora, Hook. f. ..... i.
Cunninghamii, Hook. f. ..... i.
foetidissima, Forst. ..... i.
hirtella, Labill. ..... i.
Baueriana, Hook. f. ..... i.
spathulata, A. Cunn. ..... i.

CAPRIFOLIACEÆ.

Viburnum chinense, Hook. ..... iii.

APOCYNEÆ.

Mandevillea sp.hort..... iv.

SOLANACEÆ.

Solanum sp.hort..... iv.

BIGNONIACEÆ.

Tecoma Capensis, Lindl..... iv.*

VERBENACEÆ.

Vitex littoralis, Cunn..... i.

I have counted the species of domatia-bearing plants in each order in Lundström's, Lagerheim's, and this paper, and arranged them in descending order.

Rubiaceæ, 107; Tiliaceæ, 40; Bignoniaceæ, Oleaceæ and Lauraceæ 16 each; Cupuliferæ, 15; Solaneæ, 13; Apocyneæ, 12; Rhamnaceæ, Aquifoliaceæ and Juglandiaceæ, 6 each; Loganiaceæ and Anacardiaceæ, 4 each; Caprifoliaceæ, Bixaceæ, Meliaceæ, and Rosaceæ, 3 each; Compositæ, Ribesiaceæ, and Hamamelideæ, 2 each; Asclepidiaceæ, Sapotaceæ, Aceraceæ, Myrtaceæ, Magnoliaceæ, Ulmaceæ, Platanaceæ, Sterculiaceæ, Olacineæ, Araliaceæ, Viniferæ, Saxifrageæ, and Verbenaceæ, 1 each. From the above it will be seen that the orders Rubiaceæ and Tiliaceæ are far before the others in domatia-bearing species.

There are, however, included in Dr. Lundström's list some plants which are only doubtfully possessed of these structures, and one or two which certainly are not. To take the latter first.

TECOMA AUSTRALIS, R.Br.—Dr. Lundström says (**1**, p. 37)—This plant "has 1-3 dimples which are (always ?) inhabited, but

* Remarkable as having branching hairs in the axils.

they occur in quite an indefinite manner on the under side of the leaf. I cannot assert with positive certainty that these dimples are domatia, but I may commend these particular formations to closer examination by those biologists who have the opportunity of studying them in the open." The structures alluded to occur in quite a number of plants, *e.g.*, *Cedrela australis*, *Acronychia laevis*, and many indigenous Rutaceæ. They are crater-shaped hollows, and when young the edges overhang so as to give a transverse section the appearance of such a domatium as is found in *Coprosma*. But the whole cavity is filled up by a sessile round or elliptical gland, flat-topped, shining with moisture, and pale coloured. Sometimes in old leaves the gland is wanting, having apparently dried up and fallen out. In *Cedrela* they sometimes occur on the veins, usually near the top of the leaf, and in one instance I found one in the hair-tufted depression which forms the first stage of a domatium. But ordinarily they occur away from the veins, and I could not find any rule as to the place of their occurrence. Acarids are sometimes found in them.

"Acacia dealbata, Link. (1, p. 54) has usually red dimples along the rhachis in a row on the upper side. These are most frequently uninhabited as far as I have been able to find. . . . These peculiar formations may well deserve to be closely examined in a natural state." These are most decidedly not domatia, but true secreting glands with a duct to carry off the secretion, which, judging from the fondness of ants for it, is of a sugary nature.

Quercus robur, Linn.—At the base of the leaf, there are two backward curves forming shell-shaped cavities which Dr. Lundström takes to be domatia. I find, as he describes, that there is no structure characteristic of domatia. Stomata occur inside, and the inner surface seems to transpire more rapidly than the rest of the leaf, for on several occasions I found this surface covered with a dew of condensed vapour. The interior is always much covered with dust. I found no mites in examining a large number of leaves.

Ilex spp.—Dr. Lundström describes backward curls of the edge of the leaf near the base, forming a cylindrical room, and found here the cast skins of mites. But so far as dried material could show, there was not the peculiar structure found in domatia. I have found in *Eupomatia laurina* similar structures, but could find no mites or traces of them.

Schinus spp.—These have a wing on the rhachis provided with a small tooth on each side at the insertion of the leaf, which folds over and forms a cavity. I am inclined to think that none of these structures are true domatia, and would restrict that term to cavities or depressions in the leaf surface showing the peculiar appearances described under the types I have taken. But under Dr. Lundström's definition of a domatium, viz., all those structures of plants which act as dwellings or shelters for insects and receive in turn some benefit from the latter, all these might be included.

Dr. Lundström classifies domatia into the following five groups —(1) Hair tufts at axils; (2) bending back or folding of leaf or edge of rachis; (3) dimples with or without hairs; (4) small pockets; (5) bags, &c. His group 1 corresponds with my group 4; his 3rd with my 1st, and 4th with my 2nd. His 2nd and 5th groups I have not taken to be domatia, and he does not particularly notice my 3rd or 5th groups.

I have arranged the groups of types as shown because it indicates the order of development—beginningwith the highest. The domatium usually begins either as a small hair-tuft or a depression. Then an outgrowth from the veins begins extending right across the angle. Later a ridge thickens up across the open angle and runs round to the sides, so that when all the parts are grown to full height a circular orifice is formed. This is well seen at times in *Vitis Baudiniana*, which usually has the triangular pouch, but at times forms the circular cavity in this way. As the order of types, beginning with the 5th, represents the development of the domatia in a single plant, so also it probably brings before us the order of evolution.

So far as I have looked into the matter, it appears to me that domatia are most common in plants of a southern origin. At any

rate, it is certain that all the species having very perfect domatia are so, and of these New Zealand, Lord Howe Island and Australia supply a large proportion. Out of 41 species named in my original paper, 32 were from these localities.

The most interesting question, however, is, What is the meaning and purpose of these structures? And it is a difficult one to answer. The first possibility that occurred to me was that they were pathological in their nature. But prolonged observation of the plants and study of sections convinced me that they were not so. I have seldom seen the slightest appearance of disturbance of the tissues which form the walls and roof. In Packard's Forest Insects (4) p. 554, there is a figure of a section of a *Phytoptus* gall from *Fraxinus viridis* which in outline resembles a domatium. But it is only in general features that this resemblance holds—it is quite different in details. *Phytoptus*, too, spends its life in the gall and can always be found there. But when a *Phytoptus* is found in a domatium, Dr. Lundström observes and my own experience coincides, that pathological changes are always present. In *Panax elegans* and *Morinda jasminoides* I found domatia with many Acarids—not *Phytoptus*—were diseased and altered, but it was from the mites destroying the epidermis in the one case, and in the other the appearance of the tissues was completely changed from the normal state. At the same time I found leaves with fully formed domatia, on the same twig and even at the same node, opposite, which had no mites and were quite normal. There was no doubt, therefore, that the diseased state was induced in normal tissue by the insects.

It next occurred to me that they might be glands, and as many of the plants bearing the highest type of domatia have extremely glossy leaves (*e.g.*, *Coprosma lucida*), it seemed possible that they might secrete resin or varnish. But an examination of all stages of growth showed no secretion of any sort, nor did the structure resemble that of any gland I know of, so that I abandoned this line of inquiry.

It was suggested to me that the domatia-bearing plants may at one time have been like *Banksia* and *Nerium*, *i.e.*, that their

stomata were contained in crypts in which they were sheltered from excessive transpiration by long hairs, and that under altered climatic and other conditions the stomata passed out to the general surface, leaving the pits as relics of the former state of affairs. I made a careful examination of several species of *Banksia* and of *Nerium*, but found the crypts of a totally different character, and in addition, in both genera, the crypts are evenly scattered all over the surface, while in the species under consideration they occur only in the axils of the veins, or rarely (*e.g.*, *Pennantia*) on the course of the veins and appear to have a definite relation to those organs.

Again, the solution was offered that they might be extra growths caused by the superabundance of sap at the axils. But the fact that they are found mostly in the middle axils on the midrib, and not on the lower ones, where the sap would naturally be more plentiful, bears against this, and their regular organisation and appearance I think sufficiently negatives this theory.

The purpose which seemed to me most feasible, and which I took most pains in working out, was that they might perhaps be organs for absorbing gas, vapour or water, and this seemed all the more likely from the fact that the plants possessing them are all inhabitants of moist climates, New Zealand, Norfolk and Lord Howe Islands being their head quarters. Careful experiment showed that they would not fill when the leaf was wetted, the small opening being stopped by an air bubble, nor could I, even by prolonged submersion, succeed in filling them. To be sure I was not mistaken, I tried an alcoholic stain (as it flowed freely and would leave the epidermis stained as a record) and even mopped the cavities out with alcohol to encourage capillary action, but still the liquid would not run in. Mr. Betche tells me he succeeded in filling the pouches of *Dysoxylum Fraserianum* by immersion for some hours, and he thinks the fact that dust is often found inside is an additional proof that rain does run in and carries with it foreign matter. Their position on the under side of the leaf, too, is to some extent unfavourable for their filling, so that on the whole I had to abandon the hypothesis. I also tried

experiments by waxing cut petioles, letting the leaf wilt and then weighing and immersing in water, at the same time treating leaves of the same area, weight and consistence in a similar way. I found that both kinds of leaves gained in the same ratio, from 5 to 20 per cent., so that the domatia-bearing leaves had no advantage. I tested them in the same way for the absorption of vapour in closed moist chambers, in sunlight, diffused light, and darkness. The results were contradictory in both kinds of leaves. Some gained 1 per cent., and others lost as much or more. At that time I was under the impression that stomata did not occur in the pits, but as has been shown, this was a mistaken view. For want of a quantity of material I did not experiment on these plants. But it must be remembered in this connection that the stomata are in no way different nor more abundant relatively in the pits, and as there are thousands on the free surface of the leaf, no great advantage could accrue from the presence of a few in sheltered pits.

Dr. Lundström in considering their use took up the possibility of their being connected with motile phenomena, but found that untenable. He also considered them as being perhaps insect traps, but was compelled to abandon that view also, as the mites go in and out freely. In this my experience coincides with his.

The final conclusion he came to was that we have here an instance of symbiosis between the plants and the mites, and he thinks that the production of incomplete domatia has become hereditary in these plants, the stimulus given by the arrival and presence of the mites causing the final development of the domatia. He was led to this from observing the almost universal presence of mites in the cavities—in which I cannot say that my experience coincides. I find mites sometimes, but just as often not, and in the two instances in which I found large numbers (before referred to) I found the domatia damaged by them. He claims that mites of the type figured by him do not damage the cavities, but that *Phytoptus* mites do. But in both the instances I speak of the mites were remarkably like those figured, and most certainly were not *Phytoptus*. In answer to the question of what

benefit these little animals may be to the plant, he says they eat, and as a consequence excrete and give off gases, and he thinks it probable that the excreta and gases are absorbed by the plants, which are thus benefited. He also speculates as to whether certain crevices observed in some fruits may not be domatia to shelter the mites till the young plant grows and gives them the leaf-domatia. Still another service they may do is that they may eat the spores and mycelia of noxious fungi which rest and germinate on the leaf, and in support of this he mentions having seen minute rings which were undoubtedly the chewed mycelia, and also digested spores in the excreta. Some of the strongest evidence he has to offer in favour of there being a relation of mutual helpfulness between the two is as follows.

Speaking of *Psychotria daphnoides* he says: "I have kept a specimen of this species for six years in a dwelling room. When it was brought thither the domatia were for the most part inhabited, but afterwards the mites almost entirely disappeared, partly because they were swept off with a brush, and partly banished by smoking. It was curious to observe how the uninhabited domatia on the new sprouts altered by degrees, the hair formation almost entirely disappeared, the opening widened, and the inside of the domatium passed into a shallow cup-shaped depression . . . . On some leaves the domatia have almost entirely disappeared, and the epidermis in the vein-axils has by degrees assumed the same appearance usual to the under side of the leaf. At the same time the domatia which remain inhabited retain their normal form. From these facts, it may, in my opinion, be inferred that when the corresponding organs on a sprout find no opportunity for action, *i.e.*, do not become inhabited, the domatia on the following lateral sprouts become more and more rudimentary till they disappear. Whence it follows that the importance of the domatia depends on the little creatures inhabiting them" (1, p. 15).

Speaking of the protoplasm in the cuticle of the domatia walls: "It remains to examine more closely how this protoplasm behaves in cells which lie under the excrement of mites; in some sections

it seemed considerably browner and thicker, in others again it was not distinguishable from the plasma of cells which were not covered with masses of excrement. . . . Through examination of consecutive sections of an inhabited domatium, I have proved that the inner wall is quite unhurt, not injured by punctures or bites" (1, p. 20).

Again, under *Laurus nobilis*:—"On a specimen about 2 met. high which I have kept six years in a room, and from which the mites have been removed partly by smoke and partly by means of a brush, the domatia have become by degrees indistinct, and indeed have quite disappeared from certain boughs. It has been distinctly proved by this, that where mites are absent, there the domatia have not attained their normal development and size, so that the full development of the domatia is in necessary connection with the presence of mites" (1, p. 49).

By means of carefully planned culture experiments, he attempted to prove that the domatia only came after the arrival of the mites, but partially failed, as the resulting plants did produce domatia, although fewer in number, smaller and poorer in hairs than normally. On p. 61, he says it has been plainly proved that the domatia in *Psychotria*, *Tilia*, *Laurus* and others can only reach their full development in the presence of mites, and that these being absent, the domatia do not develop fully.

After prolonged consideration of the subject, I cannot consider Dr. Lundström's theory as perfectly explanatory of the use of these structures, although I must acknowledge that I have no better solution to offer. Some of the points which have occurred to me as being against his view follow.

The mites are not always to be found in wild plants; even when the domatia are fully developed, they are often absent. Dozens of domatia may be searched and no mites found. In examining large numbers of leaves of *Pennantia Cunninghamii* I found none present in the earlier stages of the development, which is just the time when their presence is needed. I find them also in the rolled leaves: such as *Ricinocarpus pinifolius*, and in the stomatal crypts of *Banksia*, and they seem to be just as much at home there as in

the domatia. I have often seen them in cracks and crevices of the plant, as between bud-scales, or in the chink between a petiole and a stem, as has Dr. Lundström himself. But I do not think that it is necessary to consider any of these places as dwellings specially prepared for the mites. Indeed Dr. Lundström uses an apt illustration of this very point when he says it would be as reasonable to consider a wood where a hare was started as a dwelling specially formed for the hare. The fact that the two plants in which I found great numbers of mites had in the one case diseased and in the other damaged domatia is very important, especially as they were not the hurtful mites, but of the same kind as those figured as domatia-dwellers. Again Dr. Lundström takes the fact of the leaves containing most domatia being very luxuriant in growth and very healthy as proving the benefit derived from the mites. But is it not possible that the Acarids might be attracted by those very states?

On the whole, therefore, while not denying the possibility of Dr. Lundström's view being the right one, I am of opinion (and I set forth my opinion in opposition to that of so good an observer with considerable hesitation) that the whole question needs much further observation and research. The following points need special attention :—

(1). The development of the tissues in all stages of the formation of the organs.

(2). The careful determination of the species of mites found in each species of domatia-bearing plants *(a)* in a state of nature; *(b)* in plants cultivated in different countries.

There also remains much to be done in the discovery of other domatia-bearing plants, and in the habitat in which each is found.

I should have mentioned that I have never been able to find either in specimens or in figures of fossil leaves any appearance of these structures.

But Mr. Henry Deane informs me that from Gippsland he has some fossil leaves of a Coprosma-like plant which apparently show decided prominences in the principal vein-axils. As this is the invariable situation of domatia in that genus it is not improbable

that they may be these organs. That they are of great antiquity I have no doubt.

I have to thank three lady friends for translating Dr. Lundström's valuable memoir, and also Messrs. E. Betche, J. J. Fletcher, and J. P. Hill for very material assistance.

References.

(1) Lundstrom, Dr. A. N.—Pflanzenbiologische Studien. ii. Die Anpassungen der Pflanzen an Thiere. Nova Acta Reg. Soc. Sc. Upsal. Ser. Tert. Vol. xiii., Fasc. ii. (1887), No. 6.

(2) Lagerheim, G. de—Einige neue Acarocecidien und Acarodomatien. Berichte der Deutschen Botanischen Gesellschaft. Band x., Heft 10, 1892, p. 615.

(3) Trimen—Handbook of the Flora of Ceylon.

(4) Packard, Dr. A.—Forest Insects. Fifth Report of the U.S. Ent. Comm.

EXPLANATION OF PLATE.

Pennantia Cunninghami (Figs. 1-5).

Fig. 1.—Part of leaf showing arrangement of domatia on veins.
Fig. 2.—Domatium from under side of leaf (× 4).
Fig. 3.—Hair from interior of domatium (× 120).
Fig. 4.—Outline of section of domatium (× 20).
Fig. 5.—Section of roof of domatium (× 120).
a, cuticle; *b*, epidermis; *c*, hypodermal layer; *d*, palisade tissue; *e*, tannin-sacs; *f*, spongy parenchyma; *g*, lower epidermis; *h*, cuticle.
Fig. 6.—Hair of domatium, *Coprosma lucida* (× 120).
Fig. 7.—Pouch-shaped domatium of *Dysoxylum Fraserianum* (× 10).
Fig. 8.—Outline of section of domatium, *Dysoxylum*.
Fig. 9.—Outline of section of depression in leaf of *Viburnum Chinense* (× 10).
Fig. 10.—Tuft of hair in axil, *Synoum glandulosum* (× 10).
Fig. 11.—Hair of domatium, *Psychotria cymosa* (× 120).
Fig. 12.—Section of leaf, *Randia Moorei*: *a* and *b*, tannin-sacs.
Fig. 13.—Hair, *Vitis Baudiniana* (× 120).